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Self-thinning in Overcrowded Pure Stands under Cultivated and Natural Conditions[1]

(Intraspecific Competition among Higher Plants XI)

Kyoji YODA, Tatuo KIRA, Husato OGAWA and Kazuo HOZUMI
依田恭二・吉良龍夫・小川房人・穂積和夫

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Seedlings of certain plants, especially those of sun-loving invaders on denuded grounds, are known to form pure stands at excessively high individual density. As the overcrowded stands grow, the plant density becomes successively lower owing to the competitive interaction between individuals and subsequent death of the suppressed. Braun-Blanquet (1951) mentioned some examples of such density adjustment; in *Suaeda maritima* stands on a sand dune in Montpellier, for instance, the density of seedlings in early May was 2,000/m^2, whereas it decreased to only 6-8 seed-bearing plants on the same area in autumn. Only a little knowledge, however, has been accumulated on the process and ecological significance of this noteworthy community function, often spoken of as the 'self-decimation' (Lysenko, 1946) or 'self-thinning' (Shinozaki and Kira, 1956).

Sukatschew (1928) drew some important conclusions from a survival experiment with *Matricaria inodora*. The mortality of plants at the end of the experiment, as expressed in percentage of the initial plant number, was always greater in the dense culture (3 *cm*×3 *cm* spacing) than in the sparse culture (10 *cm*×10 *cm*), and also on the fertilized plot than on the non-fertilized plot. Koyama and Kira (1956) and Yoda et al. (1957) proved that the self-thinning was apparently a density-dependent process, and that a high density increased the variance of growth rate of individual plants, accerelated competitive interaction between adjacently standing individuals and finally resulted in high mortality. They further showed that an overcrowded stand could not reach sound maturity and produce sufficient seeds, unless the initial high density was significantly lowered by the self-thinning process. In case where certain conditions prevented the progress of self-thinning, the total stand collapsed before maturity due to the effect of bad weather without producing any appreciable amount of seed crop. This finding suggests the important role of the self-thinning as the self-regulatory mechanism necessary for an overcrowded population to assure sufficient seeds for the next generation, although it is in itself detrimental to individual plants.

In the present paper, the authors are going to show further details of the process of self-thinning under both cultivated and natural conditions. Some fundamental properties of the process are revealed, which, they suppose, may add important knowledges for theoretical as well as applied phases of plant ecology.

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[1] Outlines of this paper were presented at the annual meetings of the Botanical Society of Japan and the Ecological Society of Japan in September of 1955 (Hirosima) and in April of 1957 (Tokyo) respectively.

Experiments with cultivated plants

MATERIALS AND METHODS

The results of the following three experiments with cultivated plants will be considered in the first place.

Experiment I A garden variety of radish, *Tokinasi*, was cultivated in sand-filled wooden pans (35 *cm*×35 *cm*×7 *cm*) with sufficient supply of nutrient salts. Seeds were sown at six different levels of density, 181, 361, 722, 1,444, 2,888 and 5,777/m^2, on July 31, 1954. Seed grains were regularly distributed in triangular disposition. Each density level was represented by six pans. Germination percentage was quite high. Each two pans were taken from every density level on August 20, August 30 and September 16, and the density of surviving plants, fresh weight of individual plants and oven-dry plant weight per pan were determined.

Experiment II Material plant: soybean, a variety called *Tamanisiki*. Initial planting density: six levels, 14.4, 28.9, 58.1, 115, 231 and 465/m^2. Date of sowing: June 25, 1955. Date of sampling: July 16, August 2, August 24 and September 25. Two seeds per hill were planted at regular hill-intervals in triangular disposition on a fertile field in the Botanical Garden of the Osaka City University. Seedlings were later thinned to one plant per hill to assure the density levels mentioned above. The plot was 1.4m wide and long enough to include at least 30 plants excluding the border individuals. Each density level was represented by eight plots randomly arranged on the field. Experimental plots were thoroughly weeded during the period of study, but no fertilizer was applied. Two plots from each density level was sampled at a time for individual fresh weight, total oven-dry weight per plot, mortality, and other determinations.

Experiments I and II were respectively parts of the hill-planting experiments reported elsewhere (Ogawa and Koyama, 1957), serving as the control series to be compared with other series in which two or more plants were planted per hill.

Experiment III As the control in a series of mixed culture experiments, four kinds of crop, sesame, buckwheat, Sudan grass and maize were sown on June 1, 1957 at 4-5 levels of density on the field, which had been under homogeneous cover crops during the preceding seasons, at the Botanical Garden of the Osaka City Unversity. Commercial mixed fertilizer was evenly applied before sowing. The levels of initial seed density were as folows.

Sesame and buckwheat	25, 100, 2,000, 10,000 and 50,000/m^2
Sudan grass and maize	10, 100, 1,000 and 4,000/m^2

In plots with seed densities higher than 100/m^2, the number of actually germinated seedlings were somewhat less than the expected values given above. The plot size was 1.6m×1.6m in sesame and buckwheat, and 2.1m×2.1m in Sudan grass and maize respectively. Four times during the experiment at two weeks' intervals, one quarter of each plot was sampled. The plants were carefully removed from the soil, and the number of surviving plants, oven-dry weight of total plants, amounts of leaf, stem and root, and their vertical distributions were recorded. Date of the samplings was as follows.

Sesame and buckwheat	June 22, July 6, July 20 and August 3
Sudan grass and maize	June 15, June 29, July 13 and July 27

Additionally, two more plots were respectively sown with sesame and buckwheat at the initial seed density of $10,000/m^2$. One received no fertilizer application, while the other did twice as much fertilizer as the normal amount.

Results of the mixed culture experiments will be presented in another opportunity.

Results

Time trends of self-thinning in the three experiments are given as survival-time curves in Figs. 1-6. The curves were essentially similar in these six kinds of crop in spite of the considerable differences in their habits. Three principal features may be mentioned as common in all cases illustrated.

1) Self-thinning did not occur in plots where the initial plant density was lower than a certain level; the critical level was between 722 and $1,444/m^2$ in radish, about $115/m^2$ in soybean, between 100 and $600/m^2$ in sesame and buckwheat, between 100 and $800/m^2$ in Sudan grass and between 100 and $400/m^2$ in maize respectively.

2) Decrease of plant number was at first more or less slow, was accelerated in the next stage, and tended to slow down again toward the end of the experiment. The second feature was most apparent in the soybean experiment (Fig. 2) in which the plants reached full maturity at the end of the three months period.

3) Trends of the survival curves which started from different initial densities showed the convergence toward a certain density level, when the experimental period was sufficiently long. In the soybean experiment (Fig. 2), for instance, the densities of surviving plants on the four plots which started from 115-930 seedlings per m^2 were almost on the same level on the 93rd day after sowing, ranging between 96 and $154/m^2$ ($124/m^2$ in average). Similar tendency is also found in sesame (Fig. 3) and buckwheat (Fig. 4), and the converging density on the 63rd day was about 600 and $700/m^2$ respectively, despite the wide range of initial plant density ($2,000$ - $50,000/m^2$) in both cases.

The last feature is especially noteworthy, since it suggests that the pure stands of a certain plant species can not be more densely populated than a fixed limiting density, whose value is of course dependent on time or stage of development. To make the situation clearer, the relation between the initial plant density (ρ_i) and the density of surviving plants (ρ) is examined in Figs. 7-9. The ρ-ρ_i curves obtained on respective sampling dates tend to be more or less flattened toward higher initial densities and to indicate the existence of an asymptotic level of ρ. In every case, the level of this asymptote becomes lower with the progress of time. The log ρ- log ρ_i curves in sesame and buckwheat can well be fitted by the IVth type of the C-D curve (Shinozaki and Kira, 1961), and hence be given by the equation,

$$1/\rho = 1/\rho_i + \varepsilon\,, \qquad (1)$$

suggested by Shinozaki and Kira (1956). $1/\varepsilon$ represents the asymptotic value of ρ at $\rho_i \rightarrow \infty$ or the possible highest limit of plant density at each stage of growth. As shown in

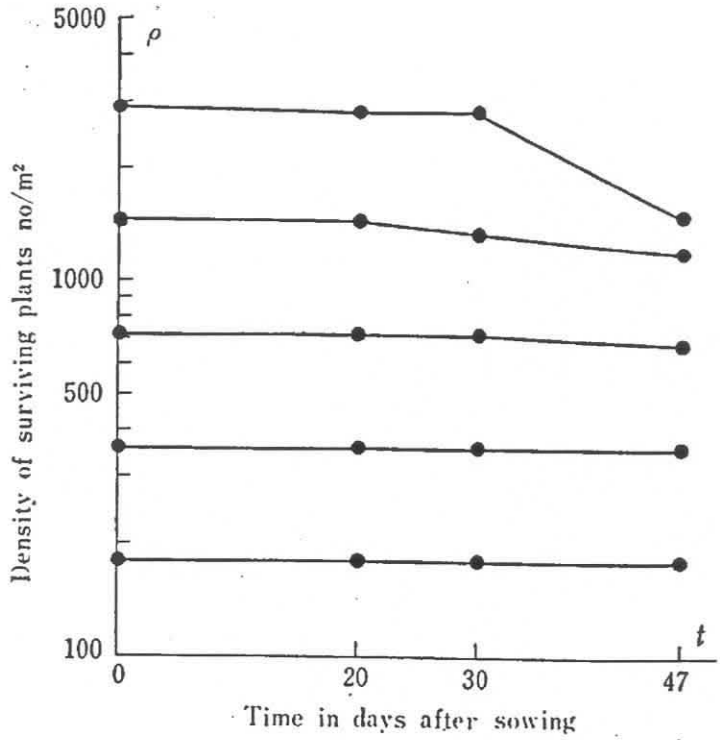

Fig. 1. Time-survival curves in radish (Exp. I). Appreciable self-thinning occured only at higher densities above 1,444 plants per m^2.

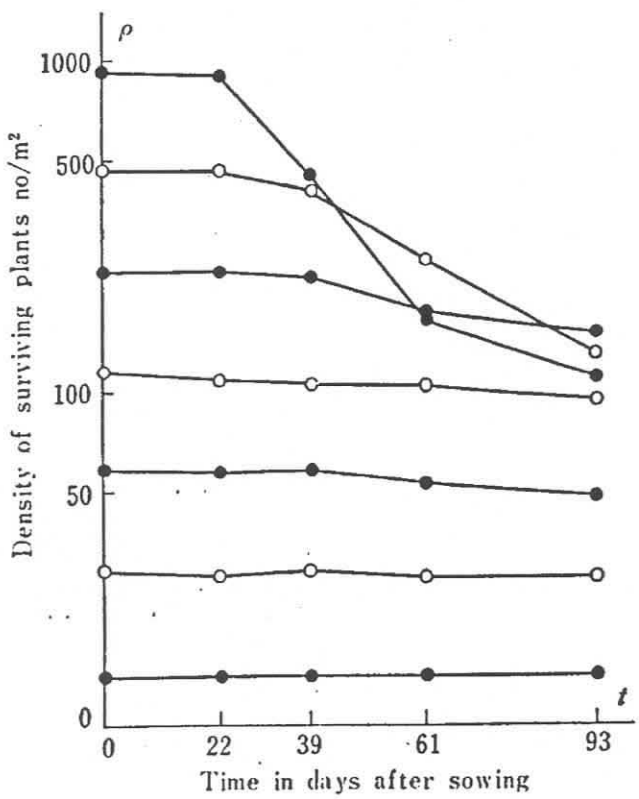

Fig. 2. Time-survival curves in soybean (Exp. II). Note the convergence of existing plant densities at the end of the experiment on the four plots which started from higher initial densities.

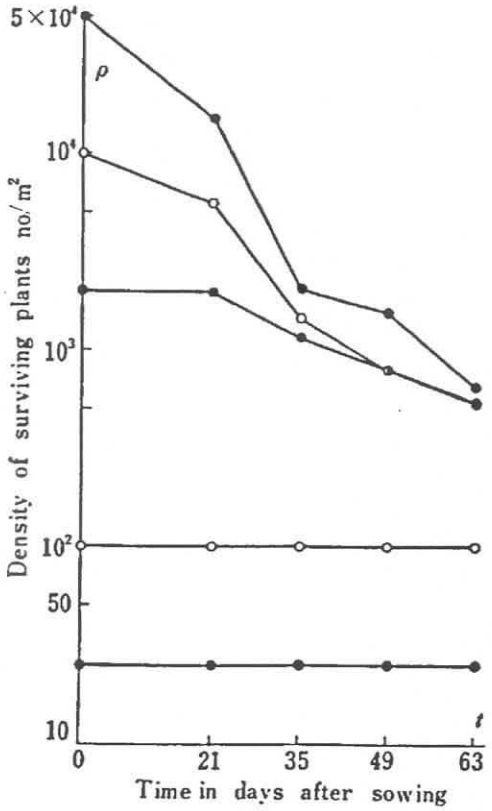

Fig. 3. Time-survival curves in sesame (Exp. III). The convergence of surviving plant density is also remarkable for the initial levels of density between 2,000 and 50,000/m^2.

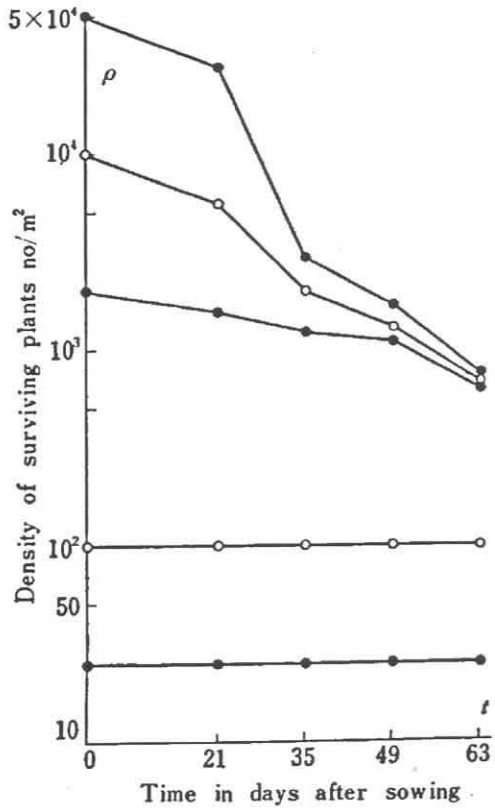

Fig. 4. Time-survival curves in buckwheat (Exp. III). The trends are almost similar to those in sesame.

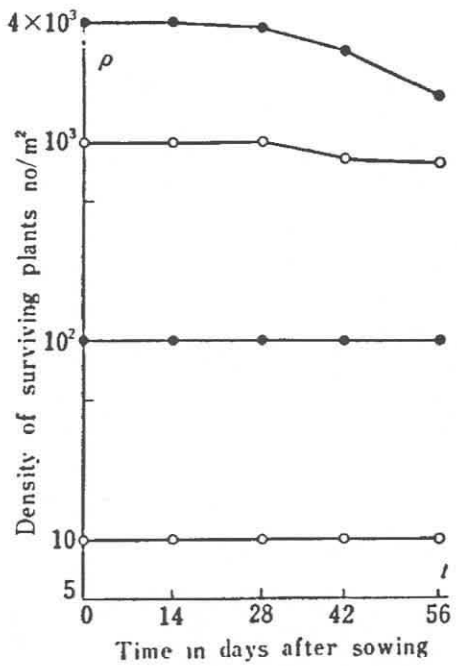

Fig. 5. Time-survival curves in Sudan grass (Exp. III). Self-thinning is less pronounced as compared with other kinds of crop.

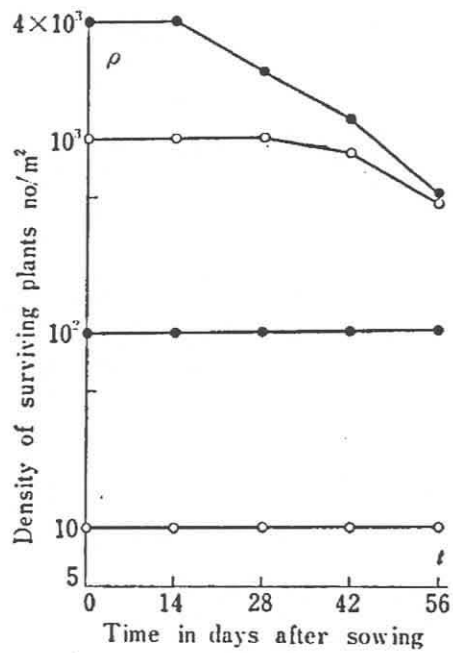

Fig. 6. Time-survival curves in maize (Exp. III).

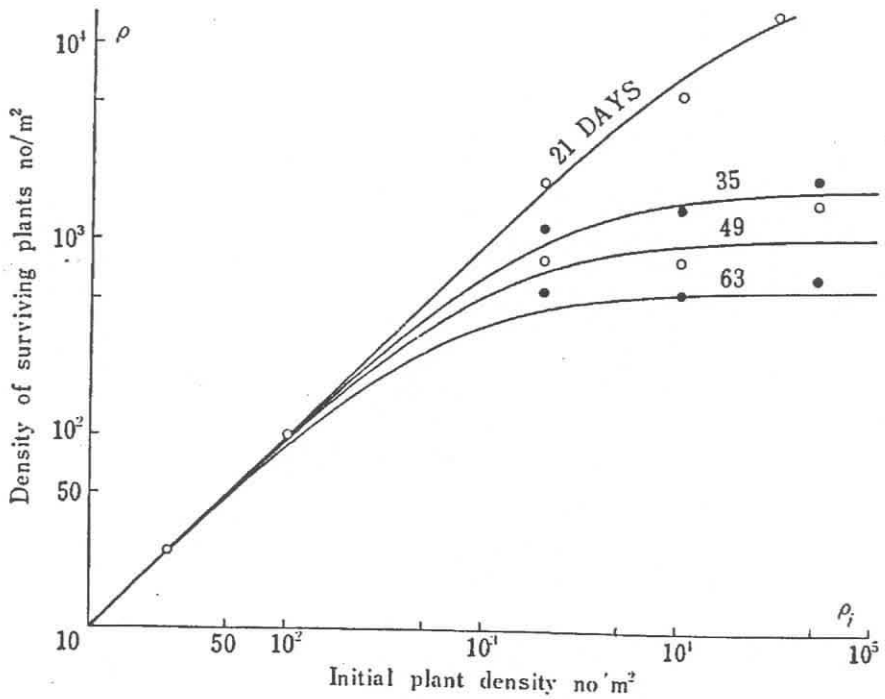

Fig. 7. The relation between the density of surviving plants (ρ) and initial density (ρ_i) in sesame. The $\rho-\rho_i$ relations are hyperbolic and give so-called C-D curves on the log-log coordinates.

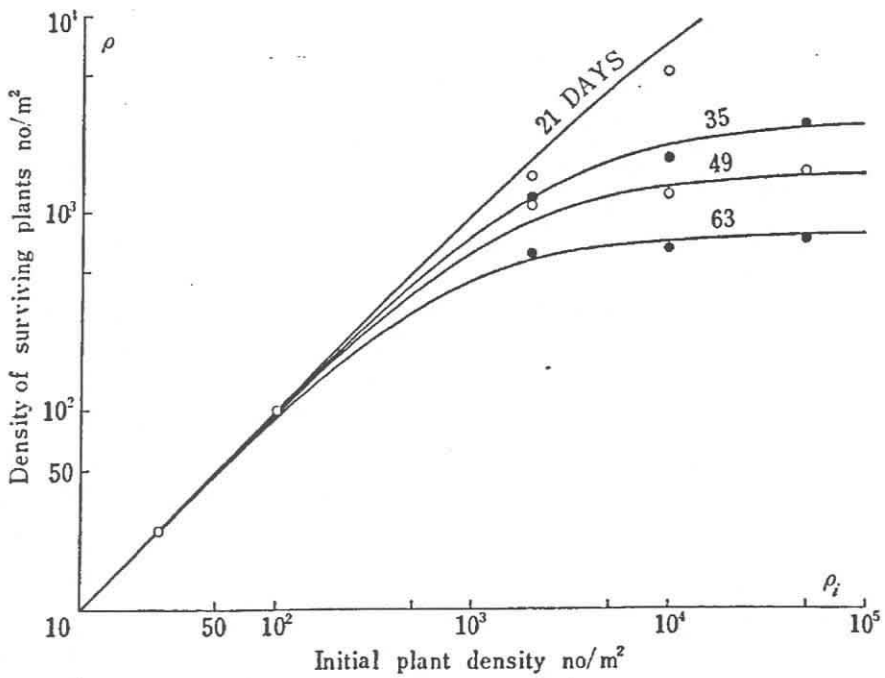

Fig. 8. $\rho-\rho_i$ curves in buckwheat. This and the preceding figure clearly illustrate the existence of an asymptotic level of ρ at each stage of growth.

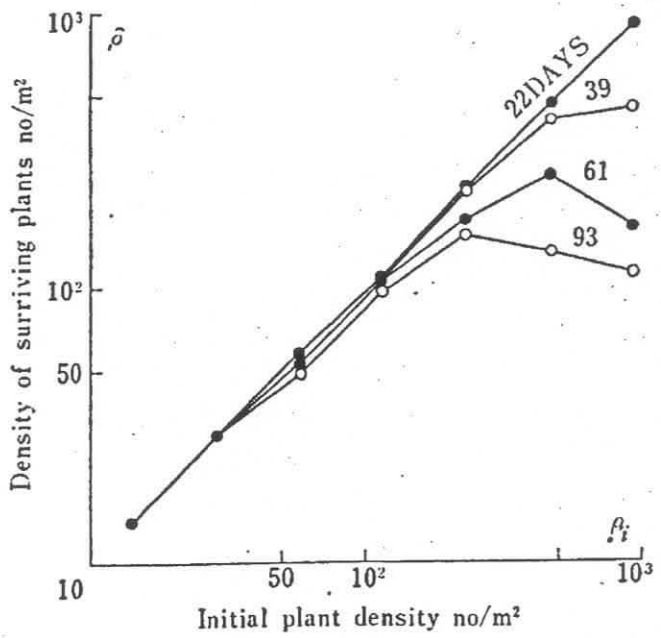

Fig. 9. $\rho-\rho_i$ curves in soybean. The curves tend to decline at the highest range of ρ_i, showing a maximum value of ρ at the middle range.

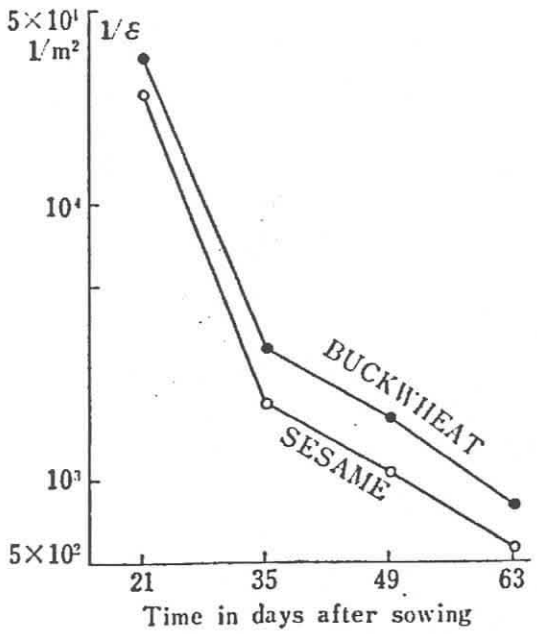

Fig. 10. Decline of the asymptotic density ($1/\varepsilon$) with the progress of time. Note the almost linear trend of the log ($1/\varepsilon$)-time curves between 35th and 63rd day that indicates the exponential decrease.

Fig. 10, the value of $1/\varepsilon$ rapidly decreased for the first week, but the rate of decrease became smaller, remaining almost constant during the next two weeks period. This means that the time-survival curves on very closely spaced plots are nearly exponential in the later half of the experimental period; viz. the density decreased approximately by half per two weeks period. In their study on the age series of *Abies* stands naturally regenerating on Mt. Shimagare, Oshima et al. (1958) found that the tree density decreased exponentially with age. Their finding well agrees with the present result.

In the case of soybean (Fig. 9), the features of ρ-ρ_i curves are essentially the same with those in Exp. III (Figs. 7-8), but the density of surviving plants tends to reach a maximum value at a certain intermediate range of initial density. The maximum value was found at $\rho_i=930/m^2$ on the 39th day after sowing, but subsequently shifted to $\rho_i=465/m^2$ on the 61st day and to $231/m^2$ on the 93rd day. Similar relations have already been reported by Harper (1960, Fig. 2) in a few species of weed poppy.

The effect of fertilizer application in sesame and buckwheat (Figs. 11 and 12) confirmed the Sukatschew's conclusion cited before. The progress of self-thinning was always more rapid on more fertilized plots. The surviving plant number on the non-fertilized plot at the end of the experiment was 1.8 times as large as that on the plot which received double amount of fertilizer in sesame, and 3.7 times in buckwheat. Average oven-dry weight of a plant, on the other hand, was 4.1 times as large in the latter as in the former in sesame, and 7.3 times in buckwheat. Namely, less fertile soil supports a larger number of small plants, whereas fertile soil does a far less number of larger individuals at the same stage of growth under overcrowded condition.

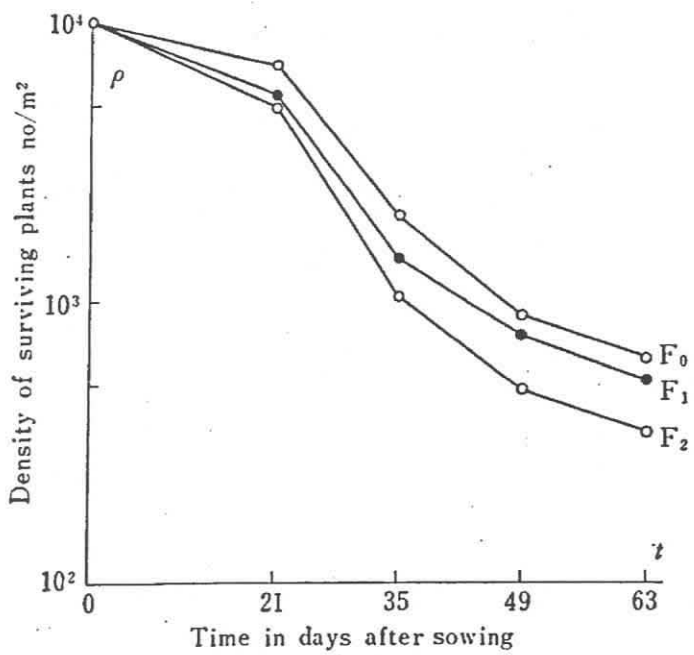

Fig. 11. Effect of fertilizer application on self-thinning in seasame. The number of surviving plants was always larger on less fertilized soil. F_0: no fertilizer. F_1: normal amount of fertilizer (Fig. 3). F_2: double amount of fertilizer.

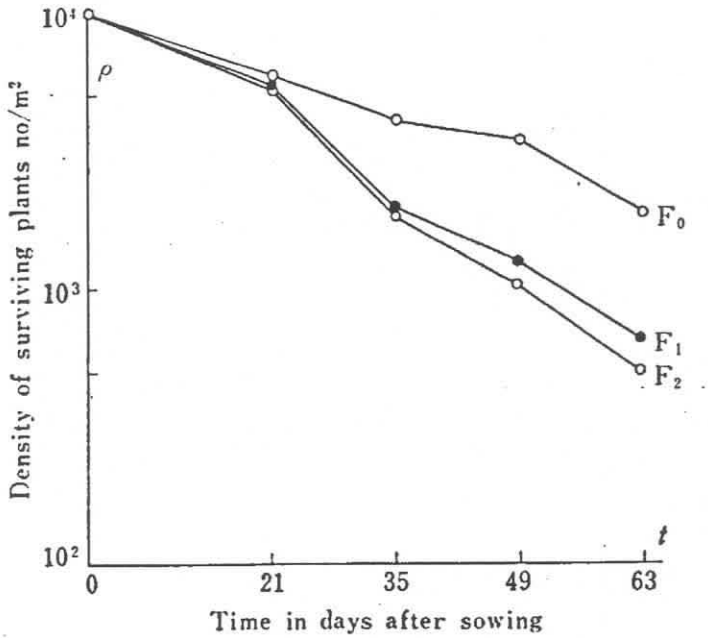

Fig. 12. Effect of fertilizer application on self-thinning in buckwheat.

In Table 1, the date on which the average size of a plant in each plot reached 0.3 g of dry weight was estimated from the growth curve, and the actual plant density on that date was in turn found out graphically from Figs. 3, 4, 11 and 12. The result reveals the very close correlation between the surviving plant density and the size of plant. Figures in the table show that the plant density on the date when the average plant weight was 0.3*g* is fairly constant in all plots where the self-thinning was actively going on, irrespective of the differences in initial density and fertilizer treatment.

Table 1. Densities of surviving plants at the time when the average plant dry weight on each plot reached 0.3 g

Fertilizer treatment	Initial density	No. of days from sowing	Surviving plant density	
			Sesame	Buckwheat
F_0	10,000/m^2	62	700/m^2	2,040/m^2
	50,000	43	840	2,150
	10,000	36	790	1,930
F_1	2,000	30	800	1,320
	100	17	100	100
	25	16	25	25
F_2	10,000	34	620	1,990

Comparing the two crops, it is apparent that buckwheat plants can be more densely populated on the same area than sesame plants of the same size, if environmental conditions are not different. Higher shade tolerance of buckwheat may possibly be responsible

for the difference. In this respect, Sudan grass seems more tolerant to overcrowding than others, as indicated by the fact that the maximum density of surviving Sudan grass plants having average dry weight of 0.3g was above 2,500/m^2. The erect habit of grass leaves, which allows light to penetrate more easily through leaf layer and results in greater thickness of leaf layer in grass communities than in herb communities (Monsi und Saeki, 1953), evidently plays an important role in increasing the maximum density possible for the plants of a certain given size. The slow rate of self-thinning observed in Sudan grass (Fig. 5) can be interpreted in the same way.

Density-yield relations in overcrowded weed communities

Common road-side weeds, with their ability of producing vast amount of seeds, often grow in pure stands at very high density. In species of *Erigeron*, for instance, seedling densities of the order of $10^4/m^2$ are not infrequently met with. Since their stands start growth at such high initial densities, the self-thinning is evidently operative throughout whole period of their growth from germination to maturity, and the density of existing plants at any stages of growth can well be expected to be on or near the maximum asymptotic level given by $1/\varepsilon$ in Eq. (1), allowed for the plants under the given growth stage and habitat conditions.

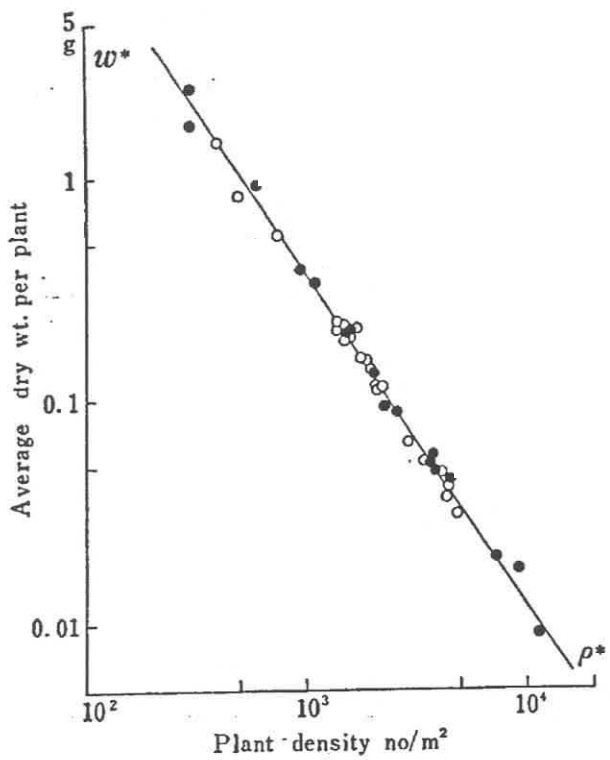

Fig. 13. The relation between the density of plants and the average plant weight in overcrowded weed stands. (1) *Plantago asiatica*. Solid circles: in Osaka City, Sep. 12, 1956. Open circles: near Kyoto City, Oct. 22, 1956.

With this expectation, pure stands of several kinds of road-side weed were investigated in Osaka City and its suburbs since 1955. Square sample plots of adequate size were placed in homogeneous pure stands, the plant number per plot was recorded, and the total yield of plants (inclusive of roots) was measured. The results are presented as the mean plant weight - density relations on the logarithmic coordinates.

A typical example obtained with *Plantago asiatica* is given in Fig. 13. Quite unexpectedly, the mean plant weight - density relation in a number of stands proved to follow a very simple curve. The stands included in the figure were investigated at two different localities and on different dates, and the age of plants might differ in respective stands since the plantain is a perenial species. In spite of the differences in age, stage of growth, locality and micro-habitat conditions, a single line represents the plant size - density relation throughout the stands. Respectively denoting the mean plant weight per plot and existing plant density by w^* and ρ^* at the state where the maximum asymptotic density has been realized by severe self-thinning, the log w^*-log ρ^* straight line in Fig. 13 can be written as

$$w^* = C \cdot \rho^{*a} . \tag{2}$$

Quite the same relation was found in other weed species such as *Erigeron canadensis*,

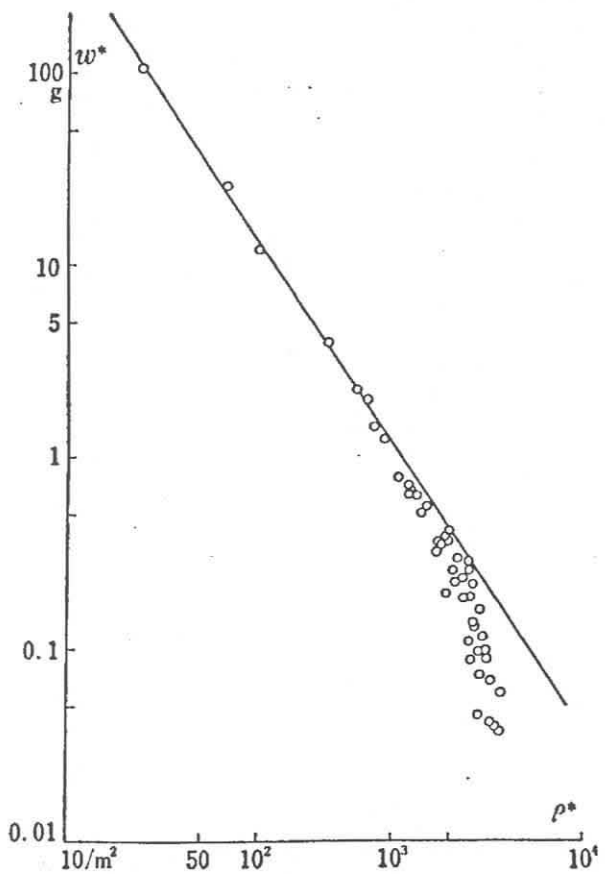

Fig. 14. (2) *Erigeron canadensis*. In Osaka, Sep. 21, 1956.

Ambrosia artemisiifolia elatior, Amaranthus retroflexus, Chenopodium album centrorubrum, etc. as shown in Figs. 14-17. Extreme differences in plant size were involved in these data. In *Amaranthus*, for instance, the largest stand exceeded 1.5*m* in average height of plant, while the smallest was barely 5*cm* tall. The log w^*-log ρ^* linearity, however, insisted to hold throughout those widely different stands

One common feature of importance in these figures is the approximate constancy of the slope of log w^* - log ρ^* line. The gradient of the lines is in every case nearly equal to $-3/2$ or -1.5 irrespectively of the difference in species. Eq. (2) can therefore be further modified as

$$w^* = C \cdot \rho^{*-3/2}, \tag{3}$$

where the value of the coefficient C differs according to the species concerned.

This rather surprising relation quantitatively represents the nature of the close correlation between the plant size and the maximum asymptotic density pointed out in the former section. Whatever the factors responsible for the plant size may be, age, edaphic

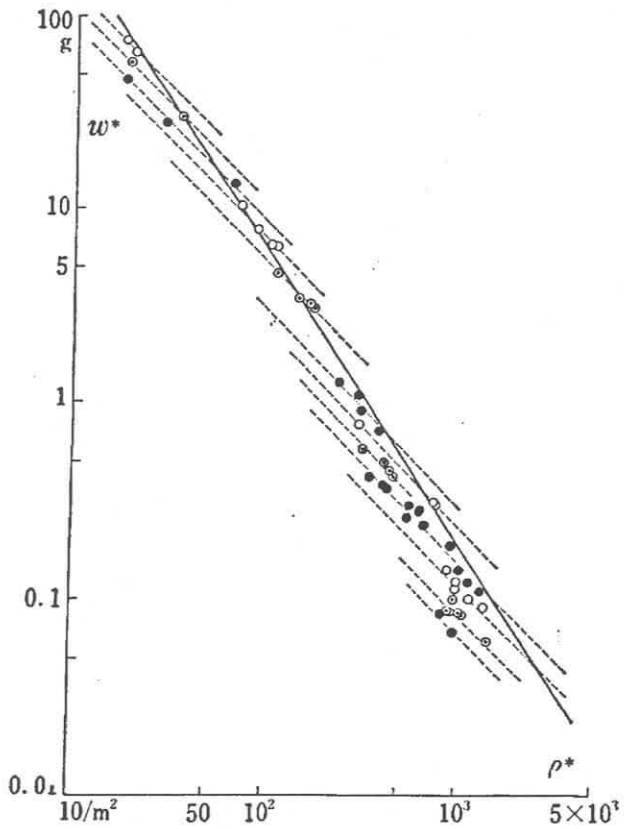

Fig. 15. (3) *Ambrosia artemisiifolia elatior.* In Osaka, Sep. 15, 1956. Dotted lines each having -1 gradient represent presumed density effect lines. Each group of stands along a dotted line should be interpreted as being in the same stage of growth and on soils of the same fertility level. Compare with Fig. 21.

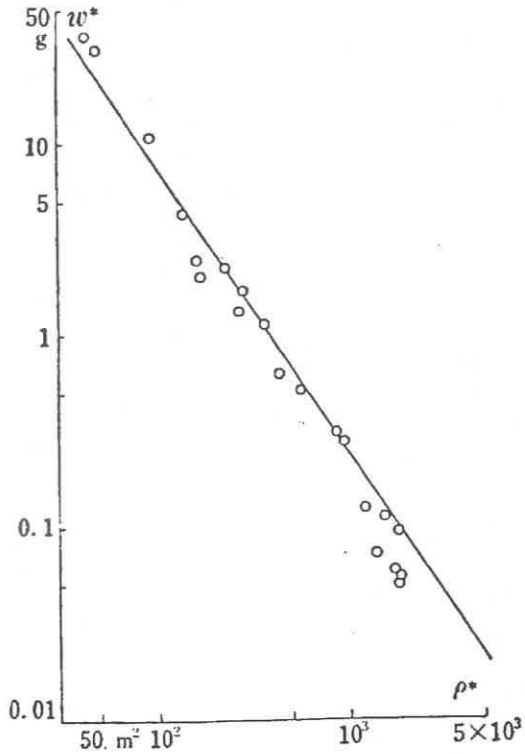

Fig. 16. (4) *Amaranthus retroflexus*. In Osaka, Sep. 14, 1956.

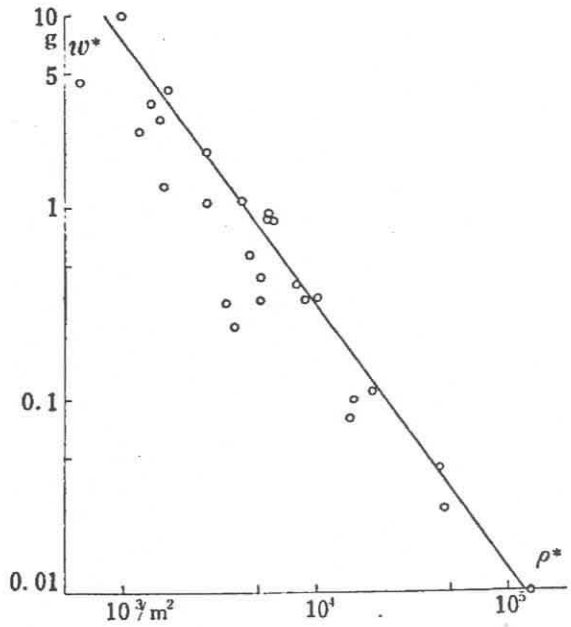

Fig. 17. (5) *Chenopodium album centrorubrum*. In Osaka, May 21, 1963.

or other habitat conditions, the possible maximum density for the plants of a given average size w^* brought about by self-thinning is expected to be equal to $(C/w^*)^{2/3}$. If the age of stands were uniform, stands on soils of different fertilities would be arranged along the line having the gradient value of $-3/2$ on the log w^*-log ρ^* diagram, those on more fertile soil exhibiting lower plant density and larger plant size. Since most of the annual or biennial weed stands are usually on the same stage of growth, it may be possible to estimate the soil fertility level by simply counting the number of existing plants per unit area. In the similar way, if habitat conditions were equal, the age difference among stands would be reflected in different situations they occupy on the log w^* - log ρ^* line. It is therefore expected that the growth of an overcrowded stand would follow the course of the line of $-3/2$ gradient specific to the kind of plant concerned. The following experiment was conducted to confirm the lastly mentioned process.

Field experiment with *Erigeron canadensis*

In the summer of 1955, a homogeneous stand of *Erigeron canadensis*, a tall composite weed of foreign origin, was found on an old field abandoned two years ago near the Botanical Garden of the Osaka City University in the northeastern suburb of Osaka. The soil was sandy and infertile, but the height of weed suggested the existence of sharp fertility gradient around an old heap of compost manure. Five square plots each $1.5m \times 4m$ in size were delimited along this gradient, and numbered 1-5 in the order of decreasing soil fertility. The plots were cleared and mixed fertilizer (ammonium sulphate 10+

calcium superphosphate 5+potassium chloride 2+magnesium sulphate 1) was applied in the ratio 5:4:3:2:1 on Plot 1 to 5 respectively in order to exaggerate the soil fertility gradient. Mature seeds of *Erigeron* were then distributed over the plots as densely and evenly as possible on October 21, 1955. The density of seeds sown was estimated to be $1\text{-}2\times10^5$ grains per square meter.

On the first sampling date (Nov. 7), 17 days after sowing, the germination was good and uniform, cotyledons completely covering the ground. During subsequent growth,

Table 2. Changes of surviving plant density in the field experiment with *Erigeron canadensis*, 1955-56

No./m^2	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Nov. 7	122,400	125,200	140,400	143,200	114,400
Dec. 16	50,300	36,200	36,250	31,400	33,550
Jan. 30	17,850	20,300	22,500	16,700	11,850
Apr. 2	5,650	7,050	9,100	8,800	8,250
May 13	2,730	3,490	4,510	5,160	5,890
Jun. 25	1,060	1,700	2,060	2,740	3,180

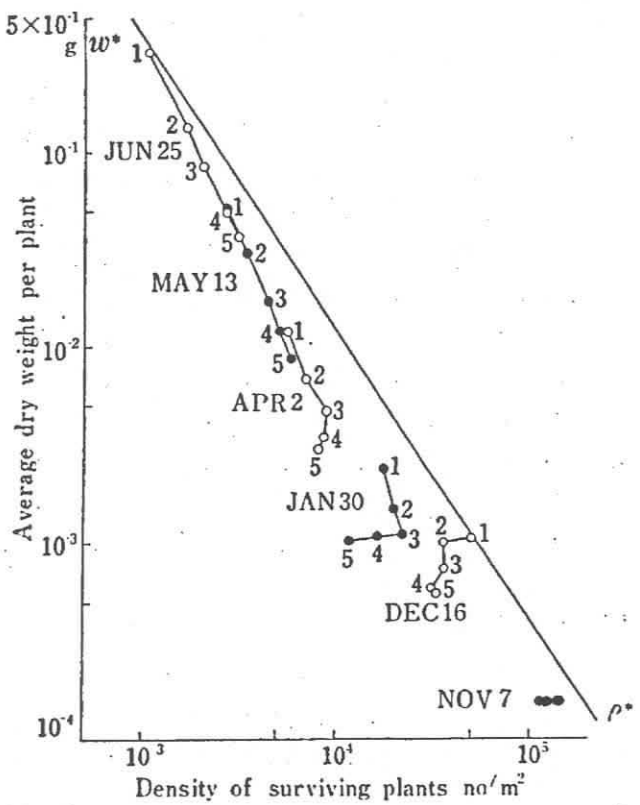

Fig. 18. Results of the field experiment with *Erigeron canadensis* plotted on the log w^*-log ρ^* diagram. Circles connected by lines represent the state of the five plots on the same sampling date. Numbers in the figure refer to plot numbers. The oblique line is based on the result of the field survey illustrated in Fig. 14.

investigations were made on December 16, 1955, January 30, April 2, May 13 and June 25, 1956. To estimate the density of surviving plants, small quadrats of $10cm \times 10cm$ ($5cm \times 5cm$ size was used only in the first sampling) were randomly placed ten times or more on the plots. Average dry weight of plant was also determined based on at least 100 individuals randomly taken from each plot. Throughout the experiment, other weed species such as *Veronica*, *Stellaria*, *Cerastium*, a few grasses, etc. found mixed with *Erigeron* were negligibly small in amount. In July, an unusually long spell of rainless days caused the death of a greater part of standing plants, and the experiment was forcibly discontinued.

The results are presented in Tables 2 and 3 and Figs. 18 and 19. As seen in Fig. 18, the initial seedling density on November 7 ($1.1 - 1.4 \times 10^5/m^2$) was near the level ex-

Table 3. Changes of total plant yield in the field experiment with *Erigeron canadensis*, 1955-56

g/m^2	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Nov. 7	19.09	19.53	21.90	22.34	17.85
Dec. 16	55.40	38.00	27.90	19.15	19.10
Jan. 30	44.40	31.50	25.90	18.50	12.40
Apr. 2	69.15	49.55	44.35	31.65	25.90
May 13	141.1	108.6	79.3	63.9	52.8
Jun. 25	353.5	231.5	175.0	139.5	120.0

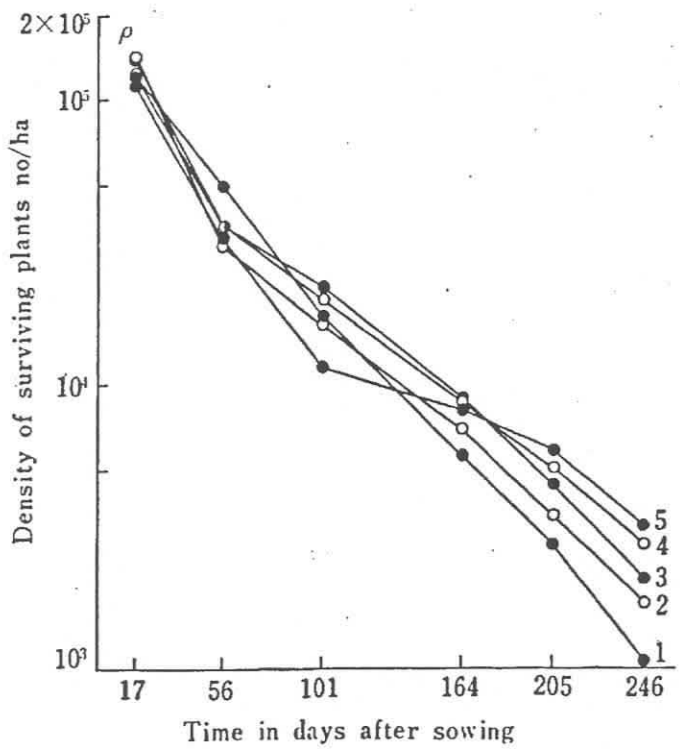

Fig. 19. Time trends of self-thinning in the field experiment with *Erigeron canadensis*. Numbers indicate the five plots.

pected from the log w^*-log ρ^* line drawn on the basis of the field survey given in Fig. 14. The effect of soil fertility became gradually apparent on the following sampling dates, and after April 2 the five plots were arranged from the bottom upwards in the order of increasing fertilizer application, approximately along the line of $-3/2$ gradient. Time trends of growth of the stands, including both the increase of plant size and the decrease of surviving plant number, also followed the log w^*-log ρ^* line specific to the species.

This result has clearly shown that the line of $-3/2$ gradient on the log w^*-log ρ^* diagram represents the locus of growth of a stand under the overcrowded condition, and at the same time the interrelation between the same-aged stands growing on different soil fertility levels.

Actual courses of self-thinning observed with the lapse of time are also illustrated in Fig. 19. The time-survival curves in the later half of the experimental period are again nearly exponential, offering another evidence for the experimental fact found in Fig. 10.

Discussion

3/2TH POWER LAW

The quantitative relation given by Eq. (3) is so universally found in various plants that it may be termed *the 3/2th power law* of self-thinning. Though the law may at first seem strange, it is not difficult to explain its mechanism on the basis of a simple geometrical model.

Let us suppose a group of pure stands of a certain plant species. Habitat conditions and age composition are more or less uniform within one stand, but may widely differ among the stands. The structure of the stands is essentially single-layered. Initial plant density is sufficiently high, so that the self-thinning is actively going on in every stand. Under these conditions, the following two assumptions are postulated to derive the model.

i) Plants of the same species are always geometrically similar in shape irrespectively of the stage of growth and habitat conditions.

ii) Self-thinning occurs only when the total coverage of a stand exceeds 100%, and so operates as to maintain 100% cover.

When the average ground area covered by a plant is denoted by s, the second assumption can be written as

$$s = 1/\rho^* . \tag{4}$$

On the other hand, the first assumption requires that

$$s \propto (w^*)^{2/3} . \tag{5}$$

From Eq. (4) and (5), Eq. (3) can at once be derived, viz.

$$w^* \propto \rho^{*-3/2} \quad \text{or} \quad w^* = C \cdot \rho^{*-3/2} . \tag{3}$$

The above conditions and assumptions may never be fulfilled in the strict sense, but the universal applicability of the 3/2th power law indicates that the model could be accepted as a crude approximation.

Eq. (3) can further be transformed as

$$y^* = w^* \rho^* = C \cdot \rho^{*-1/2}, \tag{6}$$

where y^* is the total plant yield per unit area.. This equation shows that the plant yield increases with the progress of self-thinning in spite of the decrease in plant number, and that a reduction of density by half is associated with the yield increase of 41.4%. Fig. 20 presents an example of this form of the 3/2th power law.

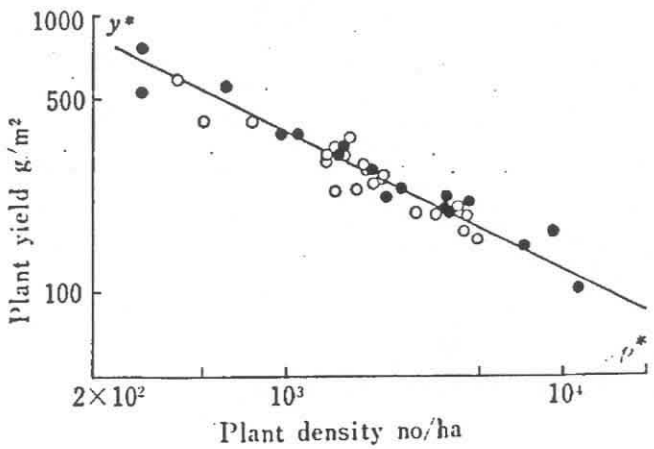

Fig. 20. 3/2th power law in *Plantago asiatica* expressed as the relation between the plant yield per unit area and the density of plants given by Eq. (6).

Relation between the 3/2th power law and the density effect law

The density effect law, that formulates the effect of plant density (ρ) on average plant weight (w) in same-aged stands grown under equal environmental conditions, is written as follows (Shinozaki and Kira, 1956).

$$(1/w) = A\rho + B \tag{7}$$

When the stands are fully grown, the coefficient B in Eq. (7) becomes negligibly small and hence $w=(1/A)\rho^{-1}$. This state is represented by a straight line on the log w - log ρ diagram. Even when $B \neq 0$, the log w - log ρ curve given by Eq. (7) may be approximated by a straight line, provided the range of density concerned is not too wide (Kira et al., 1953).

These log-log linearity caused by the density effect might be confused with the present 3/2th power law, but a strict distinction lies between the two phenomena. The density effect law is always concerned with the relation between the stands of different density which started growth simultaneously and have continued to grow under similar habitat

conditions, whereas the 3/2th power law gives the interrelation between the stands of different ages and on different habitats. In the former case, the gradient of log w - log ρ straight line ranges between 0 and —1 according to the stages of growth, and once it reached —1 after sufficiently long period of growth, no further steepening of the line's slope ever takes place (Kira et al., 1953). The slope of the log w^* - log ρ^* line in the 3/2th power law is much steeper and roughly fixed around the gradient value of —1.5.

Actual relation between the two laws is shown in Fig. 21, taking the result of the buckwheat experiment as an example. The relations between the existing plant density and the average plant weight at respective sampling dates are well fitted by the density-effect curves given by Eq. (7), no matter whether the self-thinning occured on a plot or not. The right-side ends of the density-effect curves are, however, truncated by a straight line representing the 3/2th power law, showing that the densities higher than the limit given by the line can not be realized owing to the effect of self-thinning. Thus only the overcrowded plots under severe self-thinning are situated along the line of 3/2th power law, exhibiting the similar course of stand development as found in the *Erigeron* experiment (Fig. 18).

On close examination of Figs. 13-18, it is recognized that a few points each represent-

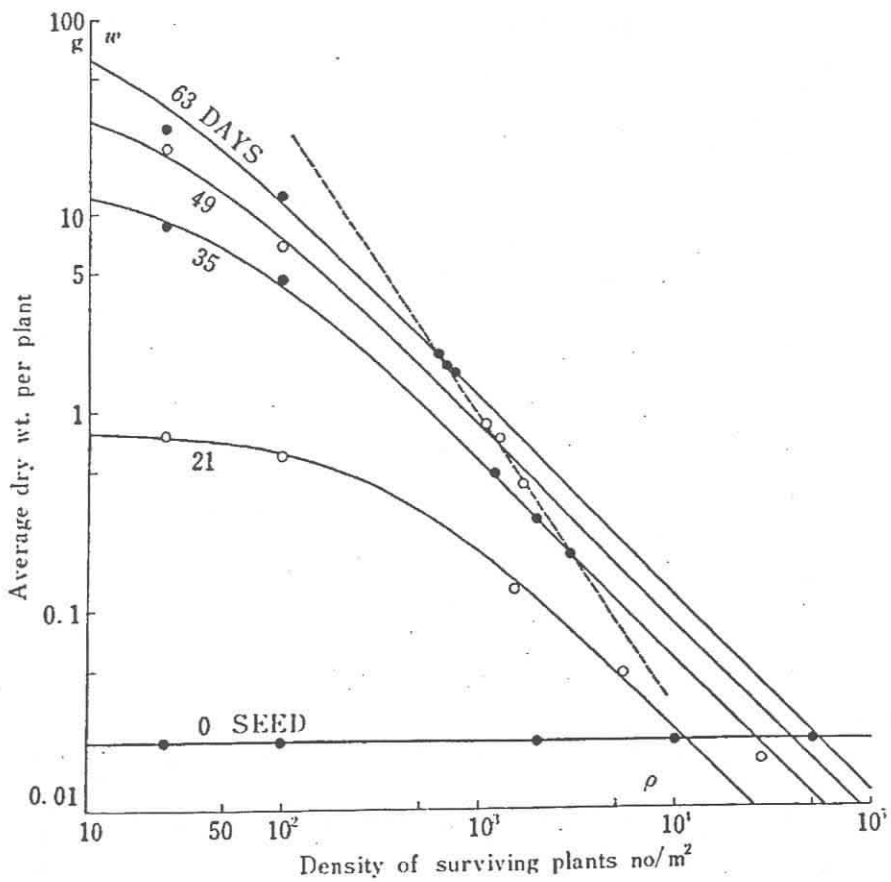

Fig. 21. Density effect curves (solid line) and 3/2th power line (dotted line) in buckwheat (Exp. III), showing the interrelation between the two.

ing different stands are often arranged on a straight line with —1 gradient, crossing the 3/2th power line, as indicated by dotted lines in Fig. 15. Most probably, such groups of points respectively represent the same-aged stands growing on soils of a same fertility level. Each dotted line should thus be considered as a partial segment of the density-effect curve, whose gradient (—1) indicates that the stands have already reached the stage of constant final yield (Kira et al., 1953) in which the coefficient B in Eq. (7) is equal to 0.

If the initial density in weed stands ranged from very low to very high level, and the competition with other species were absent, the field survey might have resulted in the plant size - density relations similar to those given in Fig. 21. In actual pure stands of weed, however, the initial density is usually excessively high, so that only the maximum asymptotic density brought about by self-thinning is realized, and only the small part of the density-effect curve near its crossing point with the 3/2th power law line can be recognized on the graph. As shown in Fig. 15, the points revealing the line of 3/2th power law are to be considered as the assemblage of those small segments of the density-effect curve.

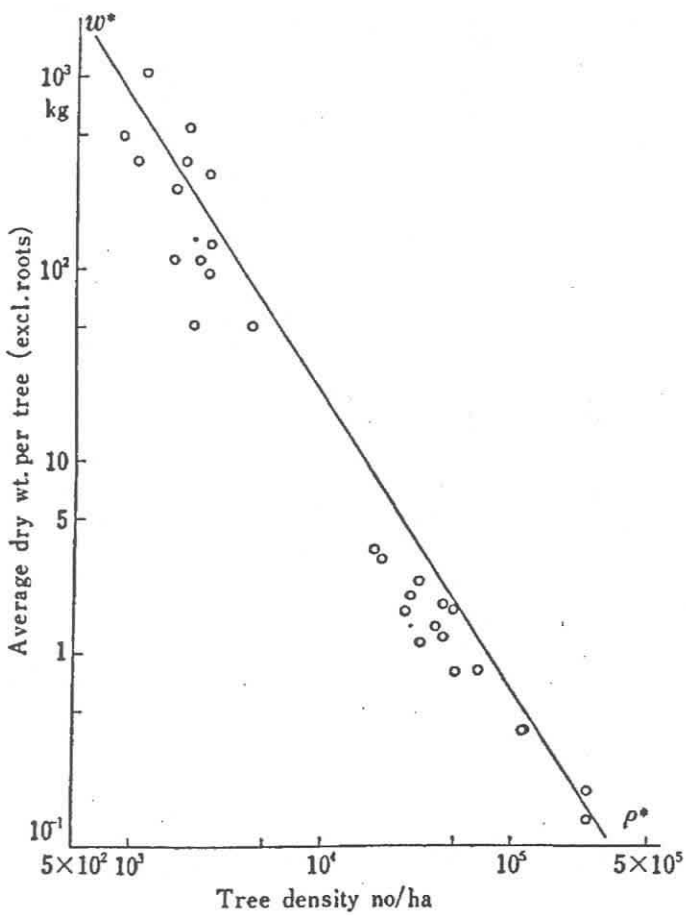

Fig. 22. 3/2th power law in natural pure stands of *Abies sachalinensis* in Hokkaidô. Unpublished data by the Research Group on Forest Productivity.

SELF-THINNING IN FOREST STANDS

It may be reasonably expected that the self-thinning process in pure stands of trees can also be understood in the same way. Three examples of the application of the 3/2th power law to forest stands are presented here. Fig. 22 concerns the pure stands of *Abies sachalinensis* in Hokkaidô, including very dense sapling stands on a coastal dune as well as fully developed stands on hill slopes, all having fully closed canopies. Natural birch stands in Hokkaidô (mixed forests of *Betula platyphylla japonica*, *B. Ermani* and *B. Maximowicziana*) are presented in Fig. 23, while the last figure was drawn based on the census of *Pinus densiflora* stands throughout Honsyû made by the Government Forest Experiment Station of Japan. Considering the error inevitably involved in the estimation of average tree size by sampling methods, the fittness of the 3/2th power law to these data seems moderate.

Similar quantitative relations between tree size and stand density have been proposed by Reineke (1933), Shidei (1956), and others. Reineke found the following formula for fully stocked pure stands of Californian red fir, Doughlas fir, Ponderosa pine, etc.

$$\log \rho^* = -1.605 \log d^* - C', \qquad (8)$$

in which d^* represents the average stem diameter at breast-height in a stand having 'full density'. If the assumption i) concerning the geometrical similarity of plant form were to be admitted, the plant weight should be proportional to d^3. This, however, is not

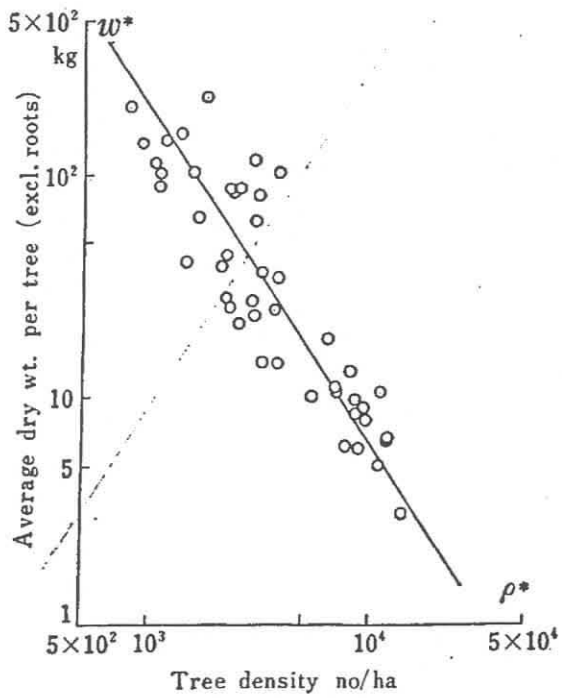

Fig. 23. 3/2th power law in natural stands of *Betula* spp. in Hokkaidô. Unpublished data by the Research Group on Forest Productivity.

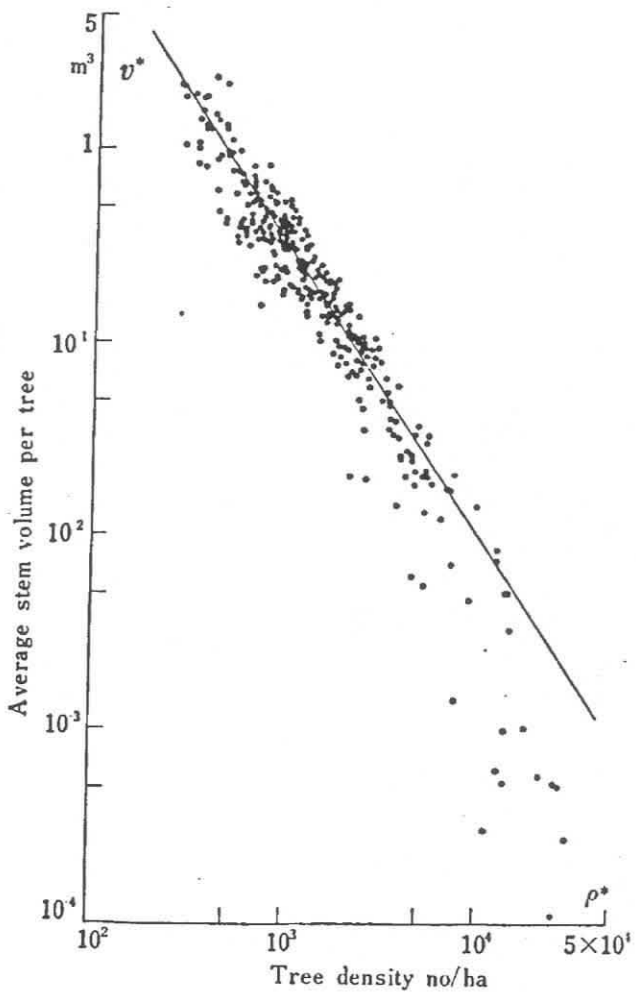

Fig. 24. 3/2th power law in natural pure stands of *Pinus densiflora* in Honsyû, Japan, drawn after the surveys made by the Government Forest Experiment Station.

always true, because the stem diameter is usually measured at a definite height above the ground independently of tree size. According to Japanese investigators (e. g. Ogawa et al., 1961), the weight of a tree (excluding roots) is in most cases approximately proportional to the 2.5th power of D. B. H. Assuming this relation for the present case, or assuming that $w^* \propto d^{*2.5}$, Eq. (7) can be transformed as

$$w^* = C \cdot \rho^{*-1.558}. \tag{9}$$

Eq. (9) is apparently very close to the 3/2th power law.

The gradient of the line of 3/2th power law is often somewhat different in different tree species. Lack of data prevents drawing exact conclusions on this point, but, generally speaking, sun-trees more closely fit Eq. (3), whereas in shade-trees the gradient of the log w^* - log ρ^* line tends to be somewhat steeper. Shidei (1956) noticed the fact that empirically established standards of thinning in tree plantations, such as the stem volume -

stand density relations given in yield tables, gave a curve on the log-log diagram more or less parallel to the 3/2th power law line specific to the tree species concerned. This fact may have an important bearing on silvicultural practice, since it means that the 3/2th power law can serve as the basis for establishing a reasonable system of plantation management. This point of view has already been discussed in some detail by Shidei (1956) and Kira et al. (1957).

Summary

1) The process of self-thinning, or the self-adjustment of excess density due to competitive interaction within overcrowded pure stands of higher plants, was analysed under both cultivated and natural conditions.

2) Trends of time-survival curves in several crop plants were experimentally examined. The results showed that the density of surviving plants at any stages of growth was hyperbolically correlated with the corresponding initial density. There is a maximum asymptotic density at each stage of growth, and the densities beyond this level can not be realized, however high the initial density was, because of the regulation by self-thinning. The asymptotic density is lowered with the progress of growth, sometimes in exponential manner.

3) As the result, the densities in heavily overcrowded plots tend to converge with the lapse of time on the same level, irrespectively of the difference in initial density. This converging density is always higher on less fertilized soil than on fertile soil.

4) The asymptotic density is closely correlated with the size of plants. Under the overcrowded condition, plants having a certain average size always maintained a more or less similar level of surviving plant density, regardless of the differences in stand age, initial density and soil fertility level.

5) Field investigations were made with a number of fully crowded pure stands of road-side weeds, under various habitat conditions and in different stages of growth. It was found that the relation between average plant weight (w^*) and plant density (ρ^*) throughout all such stands of a species could always be formulated by the equation, $w^* = C \cdot \rho^{*-3/2}$, which gives a straight line of the fixed gradient (—3/2) on the log w^*-log ρ^* diagram.

6) This relation, named *the 3/2th power law* of self-thinning, was commonly recognized in various species including several trees, and was explained based on a simple geometrical model. A field experiment with dense pure stands of *Erigeron canadensis* revealed that all of the stands, growing from widely different initial densities and on soils of different fertility levels, actually grew along a single curve given by the 3/2th power law.

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